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Mortality of *Calanus helgolandicus*: Sources, differences between the sexes and consumptive and nonconsumptive processes

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Abstract

While losses from mortality are as important as gains from reproduction in zooplankton population dynamics, the former are more challenging to quantify. We used two approaches to provide complementary insights into the mortality of a biomass-dominant copepod, *Calanus helgolandicus*, at Station L4 in the English Channel. Using a neutral-red staining method, we found that dead carcasses represented a mean of 9% of the *C. helgolandicus* copepodites sampled. The resulting nonconsumptive mortality rates are the first that have been derived for *C. helgolandicus*; and estimates suggest a contribution of 0–54% (median of 4.4%) to the total mortality rate. Consumptive mortality (i.e., that due to removal by predation), dominated for most of the year and contributed a mean of 89% to total mortality. Nonconsumptive mortality increased during summer and winter, and was positively related to maximum wind speed during the preceding 72 h, indicating that extreme weather events may lead to increased mortality. Using the Vertical Life Table approach, mortality rates across the CV-adult male stage pair were on average ~ 2.5 times greater than those of CV-adult females. Adult male consumptive mortality rates were ~ 6 times greater than those for females; adult male nonconsumptive rates were twice those of females, suggesting that predation is of greater significance to male loss rates. Summer CV-adult mortality rates were positively correlated to temperature, and to the abundance of predatory chaetognaths and siphonophores, suggesting that the gelatinous predator assemblage is the dominant agent for population control of late stage copepodites of *C. helgolandicus* at L4.

Understanding the population dynamics of zooplankton species requires the study of recruitment and loss processes. The "population gain" terms are generally logistically easier to investigate, for example, through egg production and growth experiments, and consequently, there are many more studies on fecundity and growth rates than there are on mortality. Losses from mortality are now recognized as being as important as fecundity (Uye et al. 1992; Ohman and Wood 1995; Kiørboe 1997), if not the more important factor in understanding population dynamics of zooplankton (Gallego et al. 2012). The difficulties in estimating mortality of zooplankton largely stem from it being problematic in the field to follow the same zooplankton population over time when using horizontal methods, while vertical methods require an age-abundance population structure that is not biased by shifts in recruitment strength, such as cohorts (Aksnes and Ohman 1996).

The loss of individuals from a pelagic population over time can result from various processes including advection, active emigration and the death of individuals. While the consumption of a copepod by most predators typically involves the removal of the entire animal from the water column, including consumption by fish, fish larvae, jellyfish, and chaetognaths (Bonnet et al. 2005, 2010), other copepod species (Daan et al. 1988; Boersma et al. 2014), and even via cannibalism (Bonnet et al. 2004); nonconsumptive mortality, that is mortality not caused by predation, tends not to lead to the immediate removal of the body of the animal, and hence typically results in a carcass. This nonconsumptive mortality can result from death from old age (Rodríguez-Graña et al. 2010), disease, and parasitism (Kimmerer and McKinnon 1990), the ingestion of toxic prey (Kâ et al. 2014),

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Additional Supporting Information may be found in the online version of this article.

exposure to environmental pollutants (Cohen et al. 2014; Wendt et al. 2016), and physical stresses such as during extreme weather events (Dubovskaya et al. 2005; Bickel et al. 2011; Tang et al. 2014).

While predation has been ascribed as the dominant cause of mortality in copepods (Hirst and Kiørboe 2002; Hirst et al. 2010; Daewel et al. 2014), other causes may dominate at times (Elliott and Tang 2009). The cause of death can be difficult to determine and consequently this is poorly understood for most zooplankton species. However, the combination of mortality estimates and the identification of carcasses in the water column allow us to distinguish major agents of mortality, which can perhaps best be differentiated as consumptive and nonconsumptive causes (Elliott and Tang 2011*b*). Importantly, this terminology does not equate simply to "predation" vs. "death from natural causes." Carcasses present in the water column may represent copepods that have died after being attacked or stung by predators and this mortality is included in nonconsumptive counts. Indeed, nonconsumptive sources of death can lead to a substantial proportion of zooplankton carcasses present in the water column (Wheeler 1967; Elliott et al. 2010; Elliott and Tang 2011*a*; Daase et al. 2014). Conversely, mortality estimates typically calculate removal of individuals from the water column by any means, including differential advection of the life stages as well as their consumption by predators. However, for simplicity, we hereafter define "consumptive mortality" as that highly likely to reflect removal by predators, and "nonconsumptive mortality" as that further calculated based on the proportion of carcasses present, however they died.

A topic undergoing considerable examination recently has been the strong sex skew observed in the adults of many copepod species (Hirst and Kiørboe 2002; Hirst et al. 2010); with the females at times being five or even ten times more abundant than the males (Hirst et al. 2010). This skew may arise from greater mortality of the adult males than females, especially when the sex ratios of the previous stage (CV) are on average commonly near equitable (Hirst et al. 2010). Differential mortality of the sexes in adults can result from shorter physiological longevity of males; this may for example result from the reduced feeding rates of males. Sex skew may also be attributable to differential predation in the field. Males may show riskier behavior when searching for the females, and at times they perform extravagant courtship behavior (Kiørboe 2008; Hirst et al. 2010), thereby increasing both encounter rates with, and likely detection by, predators. A combination of vital staining to determine the ratio of carcasses in the population, and the application of a Vertical Life Table (VLT) approach to determine mortality rates, has the potential to shed light on these different mortality processes that could lead to strongly skewed sex ratios.

This paper aims to elucidate mortality rates together with attribution to the causes, and to explore the temporal dynamics of the mortality of the copepod species *Calanus helgolandicus*. This temperate copepod, inhabiting the North Eastern Atlantic and fringing shelves, is experiencing an expanding distribution which has been linked to various factors, including environmental warming (Chust et al. 2014). It is an important contributor to the zooplankton biomass in these regions (Beaugrand et al. 2003, 2009; Bonnet et al. 2005), and is considered an important prey source for commercially important fish species (Heath 2007). Consequently, it is important to understand the underlying ecology and population dynamics for this species. The L4 sampling station in the western English Channel, off the coast of Plymouth, UK, is an inshore sampling site that has been visited weekly since 1988, and for which a 28-yr time series is now available. A large variety of zooplankton abundance data (including *C. helgolandicus* adult female, adult male, and copepodite densities) have been collected on a weekly basis, concurrently with a suite of environmental variables. While a recent study of *C. helgolandicus* population dynamics highlighted the dual role of reproduction and mortality (Maud et al. 2015), only one previous study has specifically examined mortality rates of *C. helgolandicus* at station L4 (Hirst et al. 2007).

Here we address the questions: (1) What are the main sources of mortality of *C. helgolandicus* at the L4 site? (2) How do these mortality sources vary between the sexes? (3) Which agents are correlated with nonconsumptive and consumptive mortality, and hence may be identified as contributing to these mortality types? Since mortality rates are difficult to quantify, and some controversy exists in the application of the particular methods (Ohman 2012), we have combined two different but complementary approaches to attempt to reveal different facets of the topic. These comprise a Vertical Life Table (VLT) approach (over 4 yr) and a carcass staining method to separate nonconsumptive and consumptive mortality (over 1 yr).

Materials and methods

Sampling at L4

Station L4 is a $\sim$ 54 m deep coastal sampling station located $\sim$ 15 km south-west of Plymouth, UK (50°15.00′N, 4°13.02′W) in the western English Channel (http://www.westernchannelobservatory.org.uk). The water column experiences seasonal stratification typically from about May to September each year (Maud et al. 2015), and often a spring and autumn phytoplankton bloom (Widdicombe et al. 2010). The station has been sampled on a weekly basis by Plymouth Marine Laboratory since 1988, initially for zooplankton and supported by an array of physical, chemical, and biological measurements (Smyth et al. 2015).

Calanus helgolandicus stage composition

Mesozooplankton sampling at station L4 is undertaken on a near weekly basis by a pair of vertical hauls of a Working Package 2 (WP2) net (200 μm) from a depth of $\sim$ 50 m to

the surface at a speed of $\sim$ 20 cm s^{-1}. The formaldehyde-preserved hauls are analyzed for the mesozooplankton as described in Atkinson et al. (2015). Copepodite stage composition of *Calanus helgolandicus* was determined for weekly samples from March 2002 to March 2004, as previously published (Hirst et al. 2007), and supplemented with new data that we collected over a $\sim$ 2 yr period, from January 2012 to December 2013. For this, the first $\sim$ 100 *C. helgolandicus* copepodites encountered while sorting one of the vertical hauls (chosen at random) were assigned to copepodite stage, with sex determined for CVI adults. A 200 μm mesh net was considered the most appropriate for quantifying the abundance of copepodites, following the recommendation by Skjoldal et al. (2012) for large calanoid copepods including *Calanus* spp., although it was recognized that stage I copepodites may be under-represented. We therefore determined mortality across 4 yr of weekly copepodite stage data from L4, albeit the two periods were separated by a decade.

Physico-chemical measurements

Based on the Conductivity-Temperature-Depth (CTD) profile at each weekly visit to L4, both mean water column temperature (MCT) and a Stratification Index (SI) were determined. The SI was calculated according to Irigoien and Harris (2003), whereby the SI was the difference between the temperature at 0 m and 30 m. Following Irigoien and Harris (2003), we defined stratification as occurring when the difference between the two depths was ≥ 1.0°C. All data sources and time periods for which the data were available are given in Table 1.

***Calanus helgolandicus* stage duration**

Stage-specific development times are required to determine mortality rates using the approaches applied here. The literature was reviewed to collate all experimentally-derived egg and copepodite stage duration data (Table 2), as well as egg to adulthood times. These data were obtained across a range of temperatures from 1°C to 15°C; however, the most frequent temperature incubations were at 8°C, 12°C, and 15°C. Available stage duration data were fitted to a temperature function (T, °C) using a Bělehrádek function (Bělehrádek and Mann 1935; Bělehrádek 1957), where a is a constant that accounts for the difference in the mean slope, α is the biological zero (the theoretical temperature at which development is infinitely long), b is the degree of the curvilinearity of the response (Corkett 1972), and D is the predicted duration (days):

$$D = a(T - \alpha)^{-b} \quad (1)$$

The function was solved using the nonlinear least squares (nls) tool in R (R Development Core Team 2012). The value for b for copepods has frequently been set at 2.05 in the literature (e.g., *see* Corkett et al. 1986) and has therefore been applied here. The function was first solved for α and a for the egg stage, as most studies derived duration data pertaining to this stage. This resulted in a value for α of -9.523, which was then used to solve for a for the remaining stages, hence assuming equiproportional development across temperature (Hart 1990). The results and data sources are presented in Table 2.

Table 1. Time series data available within the period 1988–2015, at Station L4, Western English Channel, UK; MBA is data from Marine Biological Association's Young Fish Trawl, PML is data from Plymouth Marine Laboratory WP2 sampling.

Time series	Data available
Total *C. helgolandicus* (♂, ♀, CI–CV copepodites)	Mar 1988–2015
♀ adult abundance	Mar 1988–2015 (excl. Aug–Dec 2005)
♂ adult abundance	1996–2012 (excl. 2000)
Egg production rate (EPR)	Feb 1992–2015 (excl. Jul–Dec 2000; 2001; Jan–Sep 2007)
Total reproductive output (TRO)	Feb 1992–2015 (excl. Jul–Dec 2000; 2001; Aug–Dec 2005; Jan–Sep 2007)
Total copepodite (CI–CV) abundance	1996–2015
Copepodite (CI–CV) stage composition	Mar 2002–Mar 2004; 2012–2013
Mesozooplankton abundance (including predators)	Mar 1988–2015
Total fish larvae abundance (PML)	Mar 1988–2015
Fish larvae abundance (to species; MBA)	2005–2014
Sea surface temperature (SST)	1988–2015
Mean column temperature (MCT)	1993–2015 (excl. Feb–Dec 2000; 2001)
Salinity	1992–2015
O_2 concentration	1992–2015
Fluorescence	1992–2015

Predator abundance and biomass

Mesozooplankton abundance data were collected from weekly L4 net samples (collections as described above). Taxa were pooled into broad groups, namely medusae, siphonophores, chaetognaths, and ctenophores, with total gelatinous zooplankton predators being their sum. Due to a change in analysis method, we have only used ctenophore data from 2008. Data on total fish larvae abundance were also extracted. Fish larval data were also made available from the Marine Biological Association's weekly L4 Young Fish Trawl (YFT) (2005–2014).

To estimate predator biomass, we measured L4 specimens and then applied literature length-mass conversions (*see*

Table 2. Bêlehràdek functions applied in this study to determine *C. helgolandicus* stage-specific development times (*D*, h). Egg hatching times fitted to the equation $D = a(T–\alpha)^{-2.05}$, α was determined to be −9.523. This value was then subsequently used when fitting the equation to data for all other life stages to determine *a*. Curve-fitting was performed using R (R Development Core Team 2012).

Stage(s)	*a*	α	Data sources
Egg	19,488	−9.523	Corkett (1972), Rey et al. (2001), Lopez et al. (2007), Cook et al. (2007), Bonnet et al. (2009)
CI	113,024	−9.523	Shreeve et al. (1998), Cook et al. (2007), Bonnet et al. (2009)
CII	43,106	−9.523	Shreeve et al. (1998), Rey-Rassat et al. (2002), Bonnet et al. (2009)
CIII	52,488	−9.523	Shreeve et al. (1998), Rey-Rassat et al. (2002), Bonnet et al. (2009)
CIV	58,131	−9.523	Shreeve et al. (1998), Rey-Rassat et al. (2002), Bonnet et al. (2009)
CV	101,421	−9.523	Rey-Rassat et al. (2002), Bonnet et al. (2009)
Egg–CI	289,911	−9.523	Rey et al. (2001), Rey-Rassat et al. (2002), Cook et al. (2007), Lopez et al. (2007), Møller et al. (2012)
Egg–CV	530,544	−9.523	Diel and Klein Breteler (1986), Rey-Rassat et al. (2002), Bonnet et al. (2009), Møller et al. (2012)

Table S1 in Supporting Information for sources of these equations). In total the characteristic lengths (for example medusa bell height or diameter, copepod prosome length) of 3780 individuals were measured. The length data were first divided into the seasons: spring (March–May), summer (June–August), autumn (September–November), and winter (December to February). We then used the length-mass conversions to estimate mean carbon mass per individual for each taxon in each season, this was multiplied with the respective abundance data to estimate biomass (μg C m^{-3}).

Vertical Life Table mortality rate calculations

The stage-ratio Vertical Life Table (hereafter "VLT") method was used to estimate mortality rates for each sampling event through March 2002–March 2004 and January 2012–December 2013. This method determines total mortality rates across stage pairs. We calculated mortality across the CV-adult female and CV-adult male stage pairs using the equation given by Aksnes and Ohman (1996):

$$\beta = \frac{\ln\left(\frac{N_{CV}}{N_{adult}} + 1\right)}{D_{CV}} \quad (2)$$

where β is the mortality rate across the CV-adult stage pair (d^{-1}), D is the stage duration (days), estimated here from the Bělehrádek functions in Table 2, using the mean temperature (T, °C) across depth (MCT), as measured on the day of sampling, and N is the abundance of the stage (no. per m^{-3}) as quantified from one of the 200 μm WP2 vertical hauls at each time-point. We recognize that the Bělehrádek function relates to temperature only and so does not account for periods of food limitation. To address uncertainties related to this we also calculated mortality rates using development times that were twice those predicted in feeding stages, based on the premise that food-limiting conditions would lengthen stage durations, but not typically more than this (Hirst et al. 2007). When deriving mortality for individual sexes, we assumed a 1 : 1 sex ratio in the abundance of the CV stage, and applied the abundance of adult males or females (*see* Discussion).

The use of VLT methods require a number of assumptions to be fulfilled. The first is that any transport processes influence stage pairs equally over the period of the total duration of the two stages. As the duration of stages is typically a few days, this seems a reasonable assumption. The second assumption requires that there is no trend in recruitment to the stages over which mortality is being derived (i.e., the duration of the combination of stages). In order to assess this, we explored the egg production rate data for trends over time, by identifying periods in which there was a sustained increase or decrease in egg production rates over time (Fig. S1 in the Supporting Information). An increasing recruitment rate trend will lead to an over-estimation of mortality rates and a decreasing trend will lead to an underestimate (Kvile et al. 2016). Such recruitment trends (i.e., slopes) are unlikely to influence mortality rates if they are negligible compared to the mortality rates determined. We calculated slopes ranging from −0.038 d^{-1} to 0.034 d^{-1} and assessed their contribution to the mortality rates. While ~ 90% of the CV-male mortality rates were of a magnitude where the recruitment rate trend was < 30% of the mortality rate, for the CV-female mortality rates this occurred on ~ 60% of occasions. As such, we can conclude that over much of the period of investigation, recruitment trends were unlikely to be of great significance to the mortality rates; however, we must be somewhat more cautious of the CV-adult female mortality rates.

Aksnes and Ohman (1996) suggest a method for correcting for recruitment trends (their Eqs. 14 and 15); however, we have not employed these here since we would have to assume that these recruitment trends perpetuate through all the developmental stages. We suggest that this is very unlikely to occur, especially as both experimental and field studies have shown cohorts to become less distinct and more spreadout over subsequent developmental stages (Campbell et al. 2001; McKinnon and Duggan 2003;

Kimmerer et al. 2007) , consequently, recruitment trend estimates in the egg stages are likely to be overestimates of trends in later developmental stages. While Kvile et al. (2016) recently proposed a statistical regression approach (SRA method) to take account of trends in recruitment and also advection, our data were unsuitable for this approach. We have chosen not to omit any mortality rates, but instead have indicated those data that are likely to be under- or over-estimates in Supporting Information Fig. S2. These tend to occur in the winter months, and so we have used two time periods in further analyses; (1) all months and (2) the subset of May–September to exclude the winter period where bias may be greater, and corresponds to the main population growth period and stratification of the water column.

A few negative mortality rates were calculated when applying the VLT method during this study. These can be expected using this method, but the data were not removed, as this would subject the data to positive bias (Hirst et al. 2007). As recommended for the VLT approach (Aksnes and Ohman 1996), we have averaged mortality across several sampling time-points. This was done by the application of a LOESS (locally estimated scatterplot smoother) smooth using the loess and predict functions within R (R Development Core Team 2012), set to an *f*-value of 0.2. This value was chosen to produce a smoothing in which major seasonal patterns were still evident. Regression analyses of VLT-derived mortality rates and explanatory variables used the LOESS-smoothed rates at each sampling point, rather than the actual mortality rates.

Typically, the traditional VLT method is applied using abundance data in which intact carcasses cannot be identified and removed from total counts; this may create a bias in the abundance ratios and the resulting mortality rates (Elliott and Tang 2011*b*). We apply this uncorrected approach over the entire 4 yr time span, as we do not have data on carcasses over this entire period. We do however, also apply the corrected carcass-based method for the period we have this appropriate data (i.e., January 2013–January 2014).

Total, consumptive and nonconsumptive mortality rates

From February 2013 to January 2014 on the same days that the quantitative vertical net tows were taken, we also undertook additional zooplankton collections at L4 to determine the incidence of *Calanus helgolandicus* carcasses. Collecting live samples required slow ($\sim$ 0.2 m s^{-1}), gentle oblique trawls, which we performed with a 63 μm ring net to a depth of $\sim$ 50 m. These catches were immediately stained with neutral red following the method of Elliott and Tang (2009). For this, 1 L of sample-water from the net codend was poured into a plastic container and 1.5 mL of neutral red solution (10 g L^{-1} conc.) was immediately added. The container was incubated in a water bath at sea surface temperature on deck for 15 min and afterwards sieved through a detachable 63 μm mesh. The mesh was stored in a Petri dish and flash frozen with "Freeze Spray" to instantly preserve all the zooplankton in the sample. The Petri dishes were stored on ice in a cool box for the time taken to return the samples to the laboratory ($\sim$ 2 h), and then stored in a -20°C freezer until sample processing. Chilled 0.2 μm-filtered seawater (FSW) was used to thaw the frozen sample on the mesh and rinse the sample into a conical flask. The sample was collected on a 63 μm sieve and washed into a sorting dish with $\sim$ 10 mL 0.2 μm FSW, 0.5 mL 0.1% hydrochloric acid was then added to enhance the brightness of the pink stain (Elliott and Tang 2009). Samples were examined under a dark field dissecting microscope and *C. helgolandicus* were staged, counted, and assigned to a live or dead category (bright pink/patchy bright pink areas were assessed as being alive at the time of collection; dull/pale pink were assigned as being dead at the time of collection [*see* Fig. S3 in the Supporting Information]). In some instances, various subsamples were pooled so that a total of $\sim$ 100 copepodites (stage CI to CVI) were identified.

The carcass turnover time (τ) is an important parameter in the mortality rate estimation calculations, and is a function of carcass decomposition rate and sinking losses (Elliott et al. 2010). Sinking losses may be ignored if the turbulence within the sampling site is enough to retain carcasses in the water column and enable resuspension of those that have settled (Elliott and Tang 2011*a*). Due to lack of data on sinking losses of *Calanus* at L4, we assumed for simplicity in our calculations that these were zero. Sinking losses will act to remove carcasses that should have been included, leading to an elevation in the estimate of consumptive mortality and a decrease in the estimate for nonconsumptive mortality; our estimates thus provide an upper and lower boundary of these mortality sources respectively.

Carcass decomposition time was examined by incubating freshly-killed copepodites at a range of temperatures and recording the rate of decomposition. Live *C. helgolandicus* copepodites were collected from L4, stages CIV–CVI were sorted from the catch, and placed into a Petri dish in a sealable plastic pouch. An AnaeroGen sachet (Oxoid Atmosphere Generation System) was introduced into the pouch to generate an anaerobic atmosphere and the copepods were incubated for 4 h to ensure that all were killed. They were sorted into batches of $\sim$ 80 carcasses and placed in a Petri dish with $\sim$ 10 mL 5 μm FSW from L4; this level of filtration was selected to allow microbial colonization and decomposition of the carcass, but to exclude bacterivorous protozoa that may alter the microbial community composition. The samples were incubated at one of four temperatures, which encompassed the full range usually experienced at L4 (8°C, 12°C, 15°C, or 18°C) for a period of 10–14 d. A subsample of five carcasses were removed from the incubations each day and photographed, each carcass was then categorized on a

Table 3. Explanatory variables and data sources collated for use in regression analyses with nonconsumptive *C. helgolandicus* mortality rates. PML is Plymouth Marine Laboratory, BODC is British Oceanographic Data Centre, BADC is British Atmospheric Data Centre, CTD is Conductivity Temperature Depth probe.

Explanatory variable	Categories	Source of data
Sea surface temperature (SST) (°C)	n/a	PML
Stratification Index (SI) (°C)	n/a	PML CTD
Salinity (PSU)	n/a	PML CTD
Fluorescence (no unit)	n/a	PML CTD
O_2 concentration (μM)	n/a	PML CTD
Tidal height (m)	n/a	BODC
Tide	Ebb or flow	BODC
Tidal state	Spring, neap, intermediate	BODC
Mean wind speed (knots):		
In preceding 24 h	n/a	BADC
In preceding 48 h	n/a	BADC
In preceding 72 h	n/a	BADC
Maximum wind speed (knots):		
In preceding 24 h	n/a	BADC
In preceding 48 h	n/a	BADC
In preceding 72 h	n/a	BADC

scale of 1–8 (where 1 was near transparent with no decomposition and 8 was an almost completely empty exoskeleton with minimal residual tissue; any exoskeletons collected with no residual tissue were treated as copepod exuviae, and were not counted as a carcass) (Supporting Information Fig. S4 provides a description and photographs of carcasses of the decomposition scale). A carcass decomposition time-temperature function was fitted using the time taken to reach decomposition category 8 (τ, days), against temperature (T, °C), and is described by the equation:

$$\tau = e^{-0.114T+3.51} \quad (3)$$

where $R^2 = 0.79$, $n = 20$; $p < 0.00001$ (*see* Fig. S5 in Supporting Information).

Consumptive mortality rates (β_c, d^{-1}) were derived by iteration following the equation of Elliott and Tang (2011*b*), *see* their Appendix 1:

$$\frac{N_{CV}}{N_{CVI}} = \frac{1 - \pi_1 e^{-\beta_c D_{CV}} - \pi_2 e^{-\beta_c \tau}}{\pi_1 (e^{-\beta_c D_{CV}})(1 - \pi_4 e^{-\beta_c \tau})} \quad (4)$$

where π_1 is the relative proportion of CV alive, π_2 is the proportion of CV dead, π_4 is the proportion of stage CVI dead (where dead carcasses fall within the stage categories of 1 to 8 described above and in the Supporting Information [Fig. S4], and can be discerned from live animals by the general lack of the neutral red stain), N is the total abundance of the stage(s) collected in the WP2 nets (no. m^{-3}), and D is stage duration time (days). Total mortality (β_t) was calculated using the ratio VLT method, but using corrected abundances so as they represent only those copepods identified as being alive at the time of capture (hereafter "corrected" mortality) (Elliott and Tang 2011*b*), where in addition to Eq. 4, π_3 is the relative proportion of stage CVI alive:

$$\beta_t = \frac{\ln\left(\frac{\pi_1 N_{CV}}{\pi_3 N_{CVI}} + 1\right)}{D_{CV}} \quad (5)$$

This corrected mortality rate removes the potential bias introduced by including copepod carcasses in the abundance ratios, but requires additional sampling effort and analysis.

Finally, the nonconsumptive mortality rates were calculated as total corrected mortality minus consumptive mortality rates (Elliott and Tang 2011*b*). Equations 4 and 5 were applied across the stage pair of CV and adult, deriving these separately for males and females (assuming a sex ratio of 1 : 1 in CV).

We explored relationships between nonconsumptive mortality rates and a range of variables, including SST, stratification, salinity, fluorescence (as a proxy for chlorophyll α), tidal height, tidal state (state of spring-neap cycle), and wind speed against the various mortality rates. Environmental factors and their data sources included are listed in Table 3.

Statistical analyses

Data analyses of VLT, nonconsumptive and consumptive mortality rates were performed on the weekly values. Relationships with environmental parameters (*see* Table 4 for list of physical and predator variables) were explored using the LOESS-smoothed weekly VLT mortality rates. Predator abundance and biomass data were $\log_{10}(x + 1)$ transformed before being used to minimize problems associated with nonnormality. Simple linear and backwards stepwise multiple linear regression techniques were used initially to gauge the strength and direction of any relationships (using the lm function in R). Models were checked by examining the residuals and where these were non-normal the response variable was square-root or fourth root transformed. If there was evidence of curvilinearity, a polynomial regression was applied. Heterogeneity of residuals was accounted for via the implementation of a variance-covariance structure within a generalized least squares regression model (gls function in R). Nonindependence of data was addressed by the addition of an appropriate correlation structure within a gls model. Data manipulation was undertaken using Microsoft Excel 2010. All statistical analyses were performed using the R programming environment (R Development Core Team 2012). Reduced major axis (RMA) regressions were performed using the RMA Software provided by Bohonak and van der Linde (2004).

Table 4. Explanatory variable used in regression analyses with Vertical Life Table (VLT) CV-♂ and CV-♀ mortality rates; all data from Plymouth Marine Laboratory except where indicated; MBA is Marine Biological Association.

Environmental parameter
Sea surface temperature (SST) (°C)
Stratification Index (SI) (°C)
Ctenophore abundance (no. m^{-3}) and biomass (μg C m^{-3})
Siphonophore abundance (no. m^{-3}) and biomass (μg C m^{-3})
Medusae abundance (no. m^{-3}) and biomass (μg C m^{-3})
Chaetognath abundance (no. m^{-3}) and biomass (μg C m^{-3})
Total gelatinous predator abundance (no. m^{-3}) and biomass (μg C m^{-3})
Total nongelatinous predator abundance (no. m^{-3}) and biomass (μg C m^{-3})
Total fish larvae abundance (no. m^{-3}) and biomass (μg C m^{-3})
Gadidae abundance (no. 1000 m^{-3}) (MBA)
Clupeidae abundance (no. 1000 m^{-3}) (MBA)
Pleuronectidae abundance (no. 1000 m^{-3}) (MBA)
Ammodytes spp. abundance (no. 1000 m^{-3}) (sand lances) (MBA)
Callionymus lyra abundance (common dragonet) (no. 1000 m^{-3}) (MBA)
Total fish larvae abundance (no. 1000 m^{-3}) (MBA)

Results

Overview of the L4 marine environment

Figure 1 summarizes the L4 environment as monitored during two separate 24-month periods, which were separated by a decade; March 2002 to March 2004 and January 2012 to December 2013. Sea surface temperature (SST) ranged from a minimum of 7.3°C (in March 2013) up to 18.3°C recorded in August 2003 (Fig. 1a). Stratification historically begins in May and breaks down during September (Maud et al. 2015). The years 2012–2013 followed this trend, however the earlier stratification period was somewhat curtailed, with thermocline initiation later in June 2002 extending only to August, and from May to August in 2003 (Fig. 1a).

Calanus helgolandicus reproduction appears to occur throughout the year at L4, as CI to CV stages were present through most months, except for the winter when there was an increase in the abundance of CV stages and adult females (Fig. 1b). Strong seasonal variation in *C. helgolandicus* CV and adult abundance occurred in each of the 4 yr of observations (Fig. 1c). The peak abundances of the older stages (CV–CVI) varied through March to October, and in 2013, three peaks were apparent. Total *C. helgolandicus* abundance (CI–CVI) (shown on red secondary axis; Fig. 1c) followed the same general seasonality as the CV and adult stages, but was approximately four to eight times greater. Total *C. helgolandicus* abundance was typically greater during the period 2012–2013 than in 2002–2004.

The main planktonic predators large enough to consume CV–CVI *C. helgolandicus* are presented in terms of both their abundance (Fig. 2a) and estimated biomass (Fig. 2b). It is noteworthy that the 2012–2013 period had both a greater abundance and biomass of predators than in the 2002–2004 period. Siphonophores and chaetognaths dominated all years in terms of predator abundance, although medusae were more numerous during 2012–2013 than in 2002–2003. Predator biomass patterns were somewhat different; siphonophores and chaetognaths dominated the predator biomass, but the contribution of ctenophores (abundance data available for the 2012–2013 period only) was much more marked than numerical abundance alone suggests. In addition, fish larvae biomass contributed much more to the predator biomass than to the total abundance, and their peaks occurred earlier in the year compared to the gelatinous predators. The Young Fish Trawl dataset (available for the 2012–2013 period only) revealed that larval fish predators were dominated by the Clupeidae (herring), *Callionymus lyra* (common dragonet), the Gadidae (codfishes), and the Pleuronectidae (flounders) (data not shown).

Mean monthly chaetognath abundance (in the period 1988–2015) was elevated between May and the following January (so for three-quarters of the year), with highest abundances occurring from October to December (unpublished data). There was a general increase in mean annual chaetognath abundance over this 28-yr period ($R^2 = 0.179$, $n = 28$, $p = 0.025$). Siphonophores appear at L4 from May to November, with greatest abundances between July and October. Mean annual siphonophore abundance was relatively stable over the long time-series ($R^2 = 0.007$, $n = 28$, $p = 0.674$). Medusae are generally present at L4 during May to November, with peak abundance levels in May-June (unpublished data). It is difficult to identify medusae population trends as "total medusae" incorporates so many different species, but whilst there was no trend in mean annual medusae abundance from 1988 to 2006, numbers have increased in the most recent decade of this period (unpublished data). The Ctenophora are usually present between May and July, with a peak in June. The ctenophore time-series (data available for 2008–2015 only) did not indicate any significant change in annual mean ctenophore abundance over time ($R^2 = 0.067$, $n = 8$, $p > 0.05$).

VLT total mortality

There were no significant differences in *Calanus helgolandicus* CV-adult total mortality rates (where abundance values did not differentiate live animals from carcasses) between the 4 yr (Kruskal-Wallis H statistic = 3.93, $n = 4$, $p = 0.269$) (Fig. 3). However, there were clear differences between the sexes, CV-female mortality rates ranged from 0.038 d^{-1} to 0.150 d^{-1} (mean of 0.091 d^{-1}) and CV-male rates varied between 0.044 d^{-1} and 0.446 d^{-1} (mean of 0.223 d^{-1}). The CV-male mortality rates were $\sim$ 2.5 times greater than CV-female rates (Mann-Whitney W statistic = 3621, $n = 138$, $p < 0.00001$). Both CV-female and CV-male mortality rates fluctuated over time, with summer to autumn peaks. Peaks

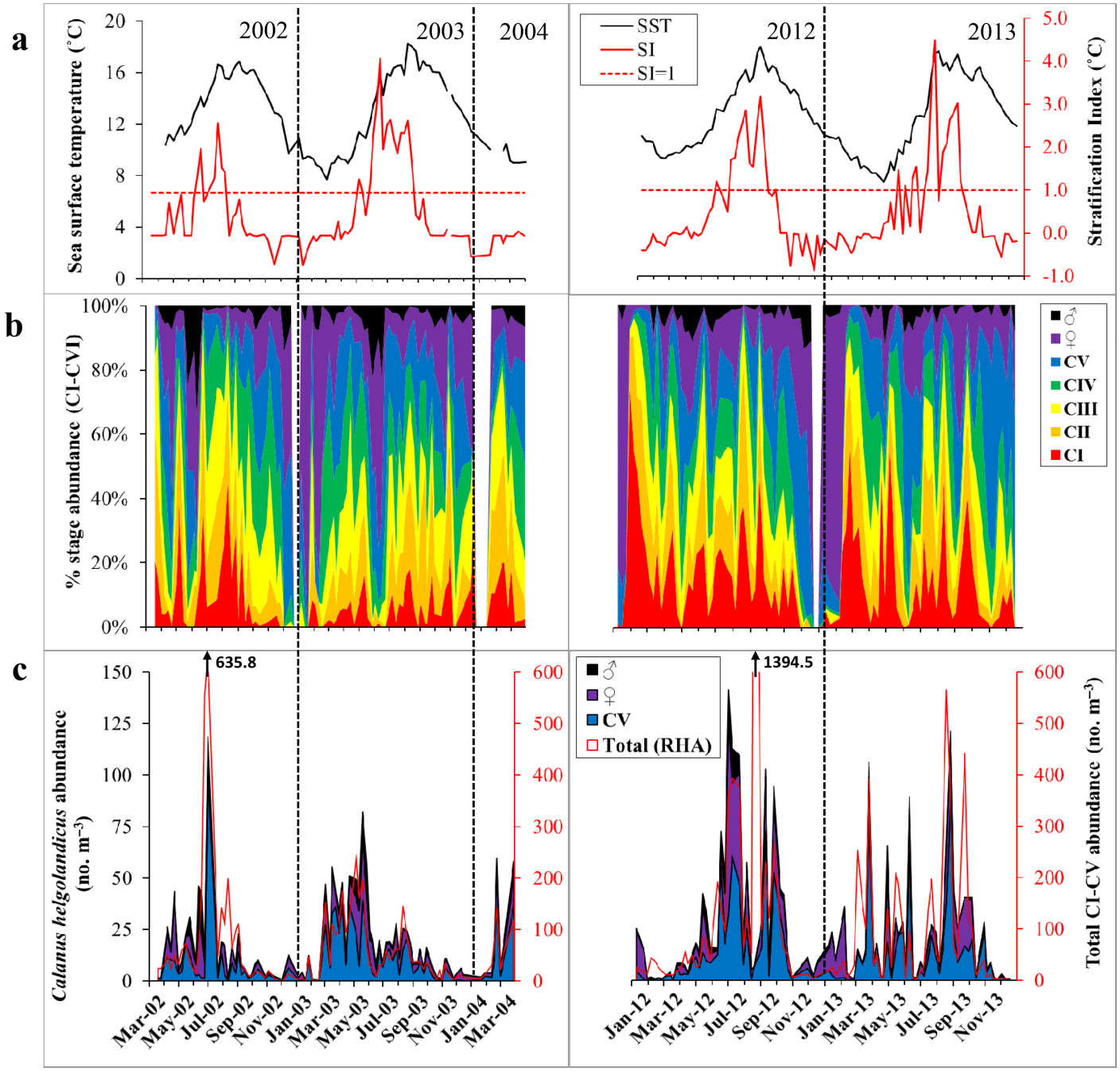

Fig. 1. The L4 environment from March 2002–March 2004 and January 2012–December 2013, (**a**) sea surface temperature and Stratification Index (right hand axis) (the difference between temperature at the surface and 30 m); the point at which stratification occurs is indicated by the dashed line and defined as a temperature difference of 1°C or greater; (**b**) *C. helgolandicus* copepodite stage composition (CI–CVI); (**c**) *C. helgolandicus* stage CV, ♀ adult and ♂ adult abundance (these presented by their addition for clarity), and total copepodite abundance (indicated by red line and right hand axis); vertical dashed lines indicate separate years.

of mortality for CV-females were less well-defined however, and also exhibited larger spring peaks during 2012 and 2013. Despite these differences, CV-female and CV-male mortality rates were highly related (Reduced Major Axis (RMA) regression analysis intercept = 0.022, slope = 0.318 (95% CI: 0.275-0.354), $R^2 = 0.542$, $n = 123$, $p < 0.00001$). The CV-female summer (June–August) and autumn (September–November) mortality rates were higher than spring (March–May) mortality, which in turn were higher than winter (December–February) mortality (Kruskal-Wallis H statistic = 30.06, $n = 169$, $p < 0.0001$). The CV-male mortality rates showed a similar pattern, but winter and spring mortalities were lowest and

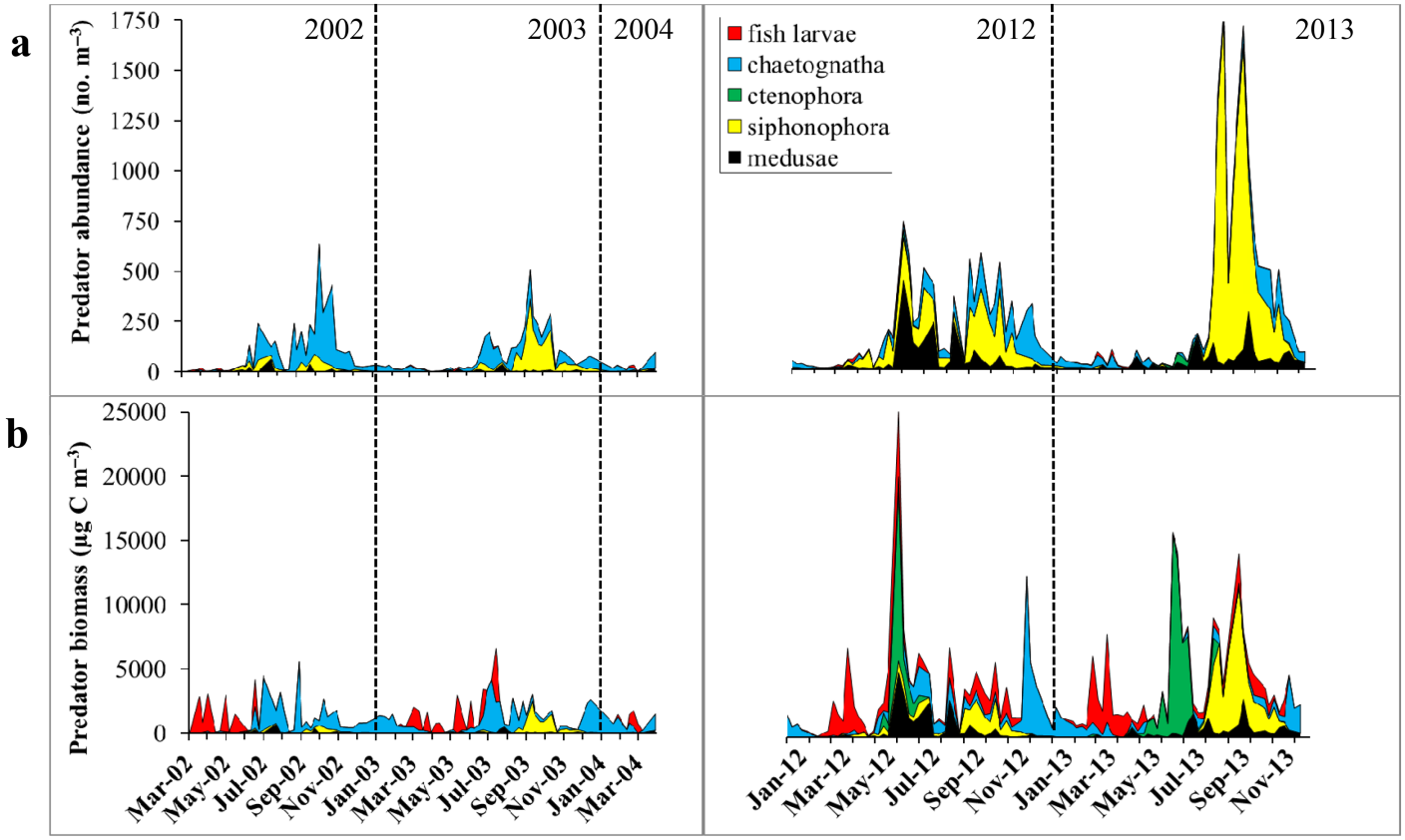

Fig. 2. The L4 environment March 2002–March 2004 and January 2012–December 2013, (**a**) main predator abundance, presented through their addition for clarity; (**b**) main predator biomass, again values added; vertical dashed lines indicate separate years. All data extracted from Plymouth Marine Laboratory's weekly WP2 sampling. Ctenophore abundance and biomass data prior to 2008 are omitted, as earlier samples have under-represented this taxon due to the samples being analyzed a long time after collection, vertical lines indicate separate years. [Color figure can be viewed at wileyonlinelibrary.com]

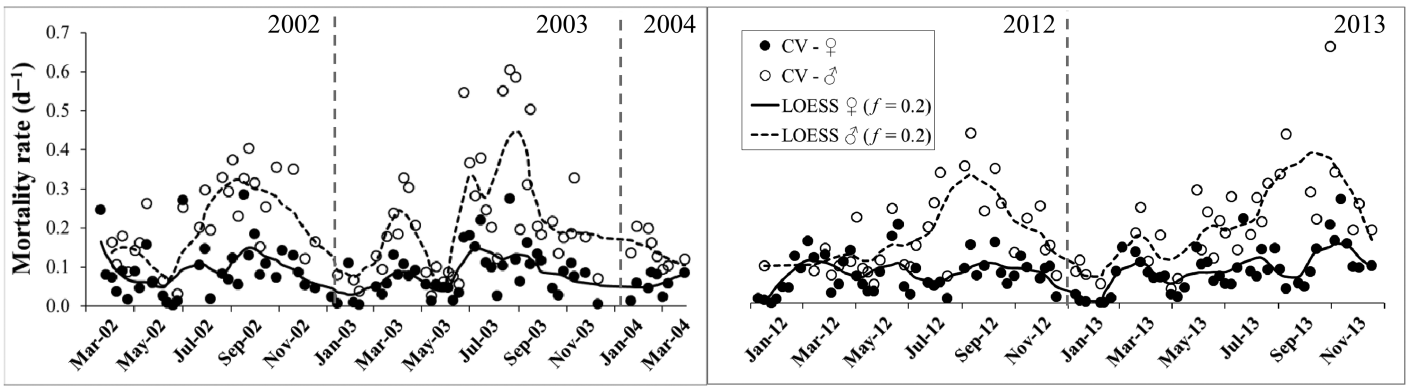

Fig. 3. *Calanus helgolandicus* mortality rates CV-♀ and CV-♂ stage pairs derived using VLT life table (VLT) method (over the periods 2002–04 and 2012–13); vertical dashed lines indicate separate years.

autumn mortalities were highest (Kruskal-Wallis H statistic = 41.78, $n = 138$, $p < 0.0001$).

To account for periods of low food availability, CV-adult mortality rates were calculated using CV stage durations twice those predicted from the Bělehrádek function. This resulted in mortality rates being exactly half those of the original calculations and therefore exhibited the same seasonal pattern as using the predicted stage durations (Fig. S6 in Supporting Information). During food-limiting periods, mortality rates may be over-estimated, but this is unlikely to

Table 5. Generalized least squares (GLS) regression analysis of mean summer (May–September) *C. helgolandicus* CV-adult LOESS-smoothed VLT total mortality rates (2002–04 + 2012–13): coefficients, standard error (SE), *t*-value, *p*-value, and AIC value for CV-♂ and CV-♀ stage pairs, single and multi-variable GLSs; SST = sea surface temperature; all abundances were $\log_{10}(x + 1)$.

Stage and Sex	Model predictor(s)	Coefficient (slope)	SE	*t*-value	*p*-value	AIC
2002–04 + 2012–13						
CV-♀						
	SST	0.006	0.001	7.254	0.00001	−454.8
	Total gelatinous zooplankton abundance	0.007	0.002	2.932	0.004	−426.8
	Chaetognath abundance	0.006	0.002	2.667	0.009	−425.6
	Siphonophore abundance	0.009	0.002	5.141	0.00001	−443.0
	Siphonophore biomass	0.008	0.001	5.615	0.00001	−466.1
	SST+	0.004	0.001	4.176	0.0002	−449.2
	ctenophore abundance	0.006	0.002	2.417	0.021	
	SST+	0.005	0.001	5.009	0.00001	−216.4
	siphonophore abundance	0.006	0.002	3.332	0.001	
	SST+	0.003	0.001	4.517	0.0001	−208.6
	ctenophore abundance+	0.006	0.002	2.703	0.011	
	siphonophore abundance	0.004	0.001	2.957	0.006	
CV-♂						
	SST	−0.252	0.041	−6.189	0.00001	−288.5
	Total gelatinous zooplankton abundance	0.025	0.007	3.475	0.001	−252.6
	Chaetognath abundance	0.018	0.006	2.769	0.007	−248.3
	Siphonophore abundance	0.026	0.005	5.673	0.00001	−269.9
	SST+	0.013	0.002	5.536	0.00001	−283.0
	siphonophore abundance	0.016	0.004	3.837	0.0003	

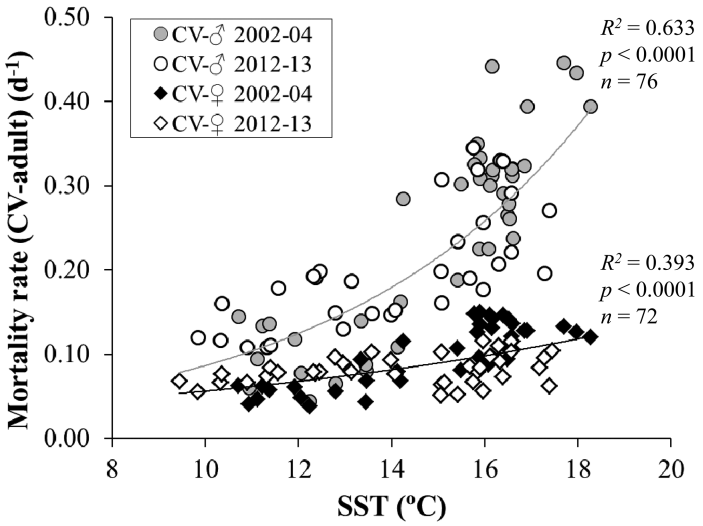

Fig. 4. Relationship between mortality rates of CV-♂ and CV-♀ stages, and sea surface temperature (SST), (covering the period May-September in the years 2002–2004 and 2012–2013); Q_{10} temperature coefficient for CV-♀ is 2.53 and CV-males is 6.17.

result in mortality outside the lower and upper boundaries we have defined.

The results of all significant relationships between predator abundance/biomass and mortality rates are presented in Table 5. Regression analyses of the LOESS-smoothed VLT mortality values (all months, 2002–2004 + 2012–2013) with SST and predator abundances and biomasses (*see* Table 4 for list of variables) found no significant relationships. Regression analyses using VLT mortality values from May to September only demonstrated that SST was a significant predictor of both CV-female and CV-male mortality rates (Fig. 4). Both CV-female and CV-male mortality rates were positively correlated with chaetognath abundance (Fig. 5a) and siphonophore abundance (Fig. 5b). Total gelatinous zooplankton abundance (the sum of chaetognath, siphonophore, ctenophore and medusae abundances) was also a highly significant predictor of mortality rates for both sexes (Fig. 5c). A stepwise backwards multiple generalized least squares (gls) regression analysis indicated that only chaetognath abundance was a significant explanatory variable, again for both sexes. When SST was included with the predator groups in multiple regression analyses, a different suite of predators was highlighted. Here, CV-female mortality rates were positively related to SST with siphonophores, SST with ctenophores and SST with both siphonphores and ctenophores. CV-male mortality rates were related to SST with siphonophores only. Biomass data for these predators were also used as predictor variables, however they provided little insight beyond that based on the abundance data.

Separate analyses of the two datasets (2002–2004 and 2012–2013) (*see* Table S2 in Supporting Information)

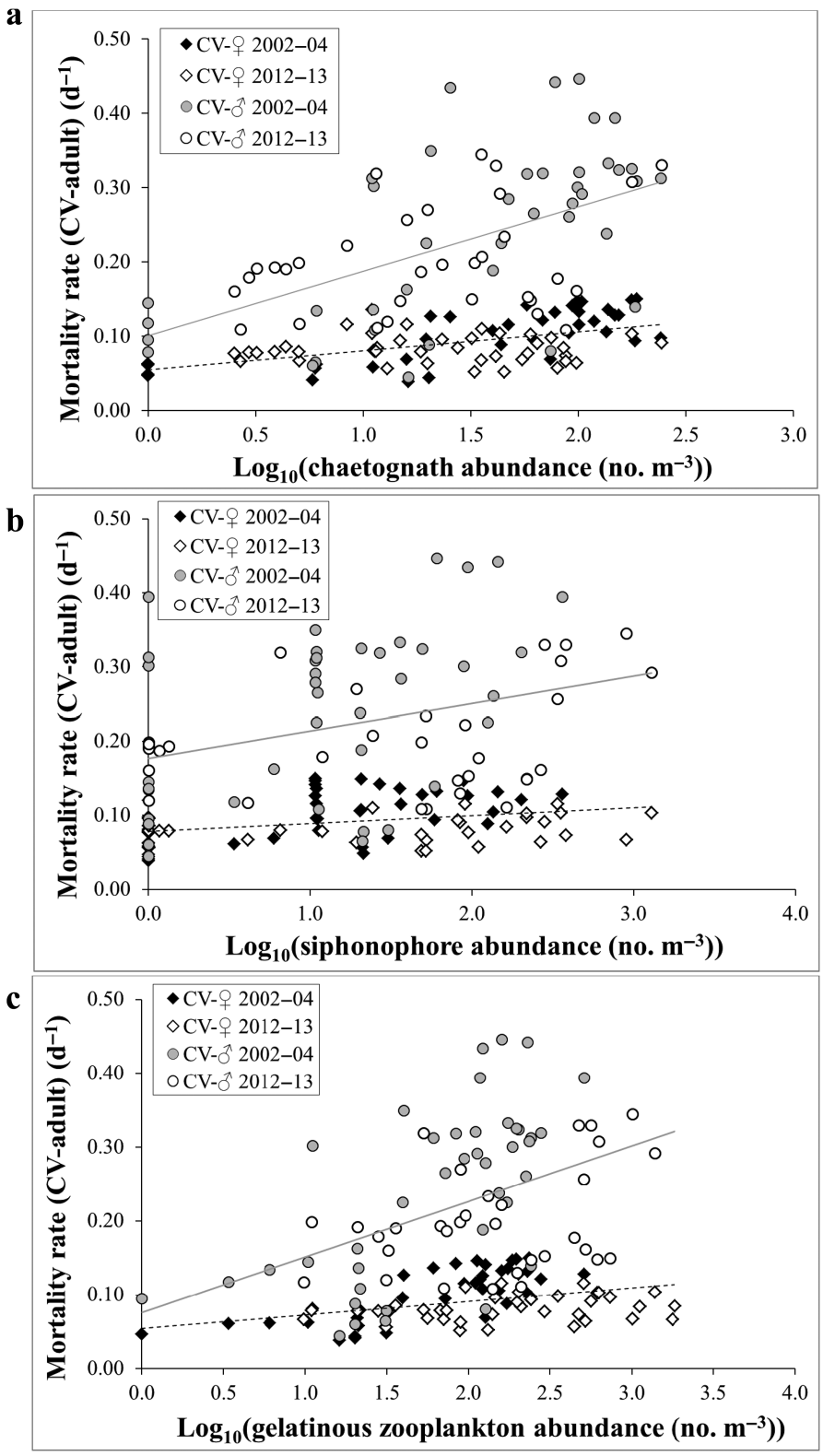

Fig. 5. *Calanus helgolandicus* Relationship between (**a**) chaetognath abundance and CV-♀ mortality rates ($R^2 = 0.289$, $n = 78$, $p = 0.009$) and CV-♂ mortality rates ($R^2 = 0.298$, $n = 72$, $p = 0.007$); (**b**) siphonophore abundance and CV-♀ mortality rates ($R^2 = 0.074$, $n = 78$, $p < 0.00001$) and CV-♂ mortality rates ($R^2 = 0.110$, $n = 72$, $p < 0.00001$); (**c**) total gelatinous zooplankton (total of chaetognath, siphonophore, ctenophore, and medusae) abundance and CV-♀ mortality rates ($R^2 = 0.157$, $n = 78$, $p = 0.004$) and CV-♂ mortality rates ($R^2 = 0.208$, $n = 72$, $p = 0.0009$), (over the period May–September in the years 2002–2004 and 2012–2013). It should be noted that if we account for the strong relationship with SST, by performing a multiple gls regression with SST + predators, the relationship with chaetognaths is lost. The relationship with siphonophores remains and a relationship between CV−♀ mortality and SST + ctenophores emerges (Table 5).

revealed that there were different predator effects between the two periods. The 2002–2004-time period showed relationships between both CV-female and CV-male mortality rates and chaetognath and siphonophore abundance, and a multiple regression analysis found that both chaetognath and siphonophore abundances together were significant predictors of CV-female mortality rates. During 2012–2013 no predator group was found to significantly correlate with *C. helgolandicus* CV-male or CV-female mortality, while medusae were the only predators with any suggestion of a positive relationship with CV-female mortality, albeit an insignificant one ($R^2 = 0.16$, $n = 38$, $p = 0.218$).

Total corrected mortality rates (Eq. 5) for 2013 were on average 0.13% greater than uncorrected rates (including carcasses), with rates ranging from 34% lower to 46% higher. However, corrected rates were not significantly different from uncorrected rates (Wilcoxon paired *t*-test: $V = 252$, $n = 56$, $p = 0.306$). This was likely due to the lack of dead carcasses (total of CV, male and female) collected in ~ 38% of samples. In addition, some corrected calculations involved similar numbers of both CV and adult carcasses, therefore the ratio of CV to adult abundance remained very similar in both corrected and uncorrected mortality rate calculations.

Nonconsumptive vs. consumptive mortality

Total copepodites (CI-CVI)–A total of 38 neutral-red stained samples of *Calanus helgolandicus* were collected throughout 2013. All copepodite data were pooled and samples with a low abundance (< 30 total [live and dead] individuals) were excluded from further analysis. A total of 31 weeks of data were then available for further analyses (with a median of 95 copepodites enumerated from each sample). Carcasses constituted 0% to 22% (mean of 9%) of the total copepodite (CI–CVI) abundance (including live-stained individuals and dead carcasses) (Fig. 6a). No carcasses were found during seven out of the 38 sampling events; these zero carcass events happened throughout the year and were not restricted to any particular season.

Consumptive mortality rates for CV-adults were typically much greater than nonconsumptive rates (Fig. 6b). The former varied from 0.003 d^{-1} to 0.123 d^{-1} with a mean of 0.062 d^{-1}. Consumptive rates contributed on average 89% to the total mortality, with a range of 46% to 100%. Nonconsumptive mortality rates were often over an order of magnitude less than consumptive mortality rates, ranging between 0 d^{-1} and only 0.02 d^{-1}, with a mean of 0.005 d^{-1}. Nonconsumptive mortality was responsible for an average of 11% of the total (median of 4.4%), but varied between 0% to 54% (Fig. 6c). Seasonal patterns indicated an upturn in the contribution of nonconsumptive mortality to total mortality during late spring and summer, with a decline during autumn, before a sharp increase once again in winter. Of course, the proviso regarding these rates is that if we have missed carcasses due to their sinking out of the water column, then our nonconsumptive and consumptive mortality rates are lower and upper limits to the true values, respectively.

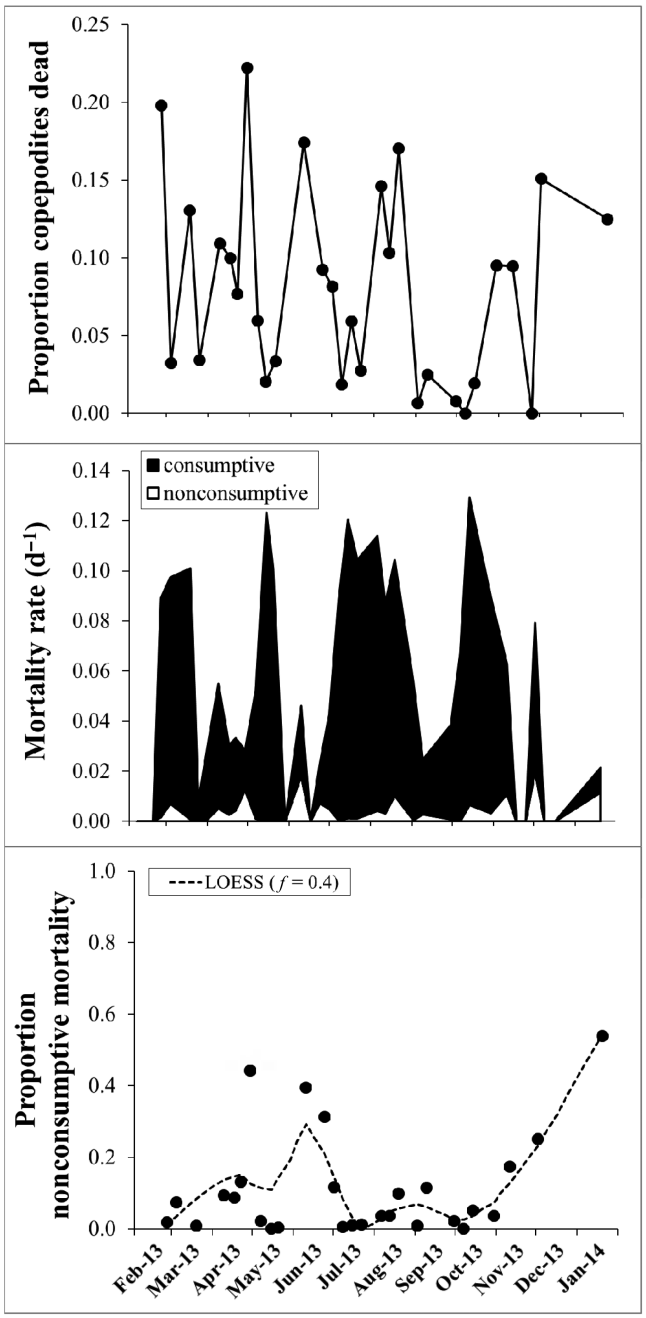

Fig. 6. *Calanus helgolandicus* copepodite nonconsumptive mortality at station L4 (February 2013–January 2014). (**a**) proportion of total copepodites (stages CI–CVI) collected which were classified as dead (not stained by neutral red stain) from weekly sampling; (**b**) nonconsumptive and consumptive mortality rates (stages CI–CVI), presented through their addition for clarity; (**c**) proportion of nonpredatory mortality in relation to total mortality (stages CI–CVI), and LOESS smooth (black dashed line).

Simple linear regressions indicated that CV-adult nonconsumptive mortality rates were positively correlated with all

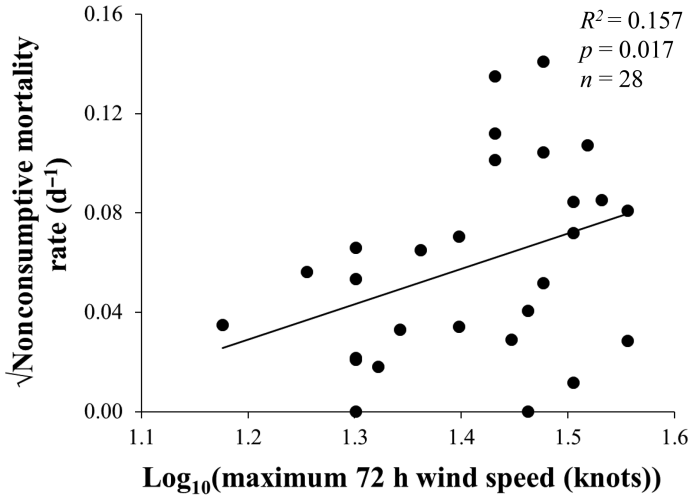

Fig. 7. Relationship between maximum 72-h wind speed and nonconsumptive mortality rate of *C. helgolandicus* copepods (stages CI–CVI) (2013), station L4, Plymouth, UK.

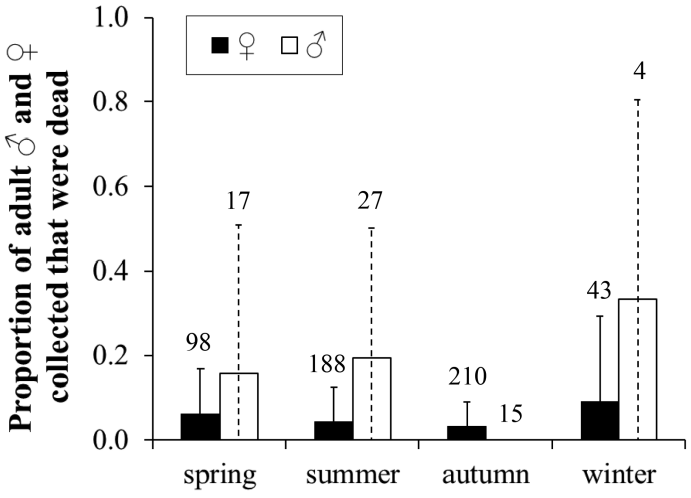

Fig. 8. Proportion of total *C. helgolandicus* adults which are dead, separated into ♀ and ♂ adults (filled bar represents ♀; white bar represents ♂) and season (spring = March–May; summer = June–August; autumn = September–November; winter = December–February). Values are seasonal means during 2013, with error bars representing standard deviations; numbers above bars indicate *n*.

three of the maximum wind speed variables (occurring over the preceding 24-h, 48-h, and 72-h), although only the maximum 72-h wind speed was significant and explained around 16% of the variation (Fig. 7). None of the mean wind speed variables indicated any relationships. We also found that none of SST, SI, O_2 concentration, salinity or fluorescence were predictors of nonconsumptive mortality. Additionally, there was no evidence of a significant influence of tidal state, either in terms of a flow or ebb tide, neap, spring, and intermediate tides or tidal height, on mortality rates.

Comparison of the sexes (CV-female and CV-male)

The proportion of *Calanus helgolandicus* adult male carcasses (13.4% of the adult male population) was greater than the respective value for females (5.5% of the adult female population). This was the case at all times of year except autumn, when no male carcasses were found in the samples (Fig. 8). Annual mean nonconsumptive mortality rates were 0.01 d^{-1} and 0.02 d^{-1} for CV-females and CV-males respectively, and annual mean consumptive rates were 0.06 d^{-1} and 0.21 d^{-1}, indicating that CV-males were subject to both higher consumptive and nonconsumptive mortality rates than CV-females. Consumptive rates contributed more to total mortality than nonconsumptive rates for both sexes; accounting for an average of 86% for CV-males and 76% for CV-females. The greatest consumptive mortality rates occurred in autumn for CV-males, whereas rates were relatively stable across seasons in the CV-female stages (Fig. 9). Nonconsumptive mortality was greatest during the summer and winter months, for both sexes. It should be noted that the number of adults counted, whether alive or dead, was very low (i.e., < 20 individuals) for $\sim 25\%$ of sampling events (most frequently during winter weeks), so we urge caution with these data.

The results of all significant mortality regression analyses are presented in Table 6. The CV-male consumptive mortality rates were related both to chaetognath and siphonophore abundance individually, and siphonophore + medusae abundance combined in a multiple gls regression. Temperature was a significant predictor of CV-male ($R^2 = 0.36$, $n = 17$, $p = 0.027$), but not CV-female consumptive mortality. When the relationship between SST and CV-male consumptive mortality was accounted for, medusae abundance was the only significant predator variable ($R^2 = 0.54$, $n = 17$, $p = 0.002$). The CV-female consumptive mortality was related to chaetognath abundance only. Neither CV-male nor CV-female nonconsumptive mortality rates were significantly related to any of the environmental factors tested, including SST.

Discussion

The two mortality methods provided complementary insights into the loss dynamics of *Calanus helgolandicus*. Mortality was calculated over various temporal scales, including over 4 yr (CV-adult VLT) and seasonal over 1 yr (consumptive vs. nonconsumptive). We discuss these in combination and focus on agents of total mortality, nonconsumptive mortality rates, and causes and differences in mortality rates between males and females.

Total mortality in relation to temperature and predators

VLT total mortality rates were highest during summer and autumn, lowest in winter, and rates for both males and females followed similar seasonal patterns, albeit with different absolute rates.

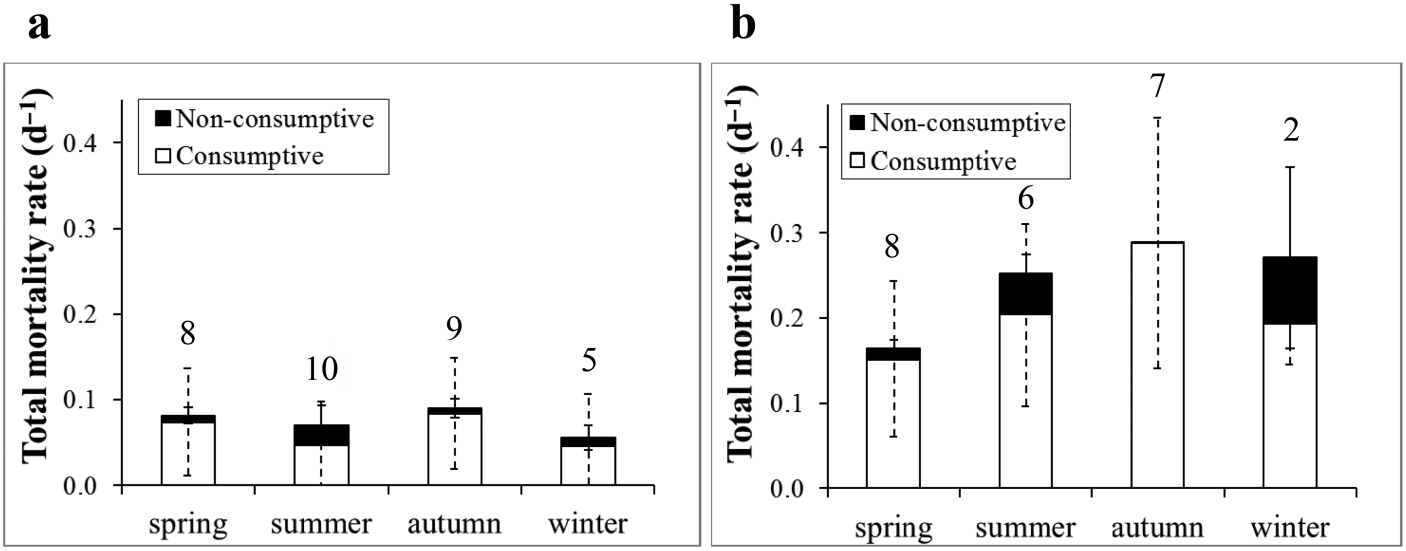

Fig. 9. *Calanus helgolandicus* total mortality rates, divided into the consumptive (white bar) and nonconsumptive mortality rates (filled bar). Values are seasonal means during 2013, with error bars representing standard deviations for each of the two mortality components. (**a**) CV-♀, and (**b**) CV-♂. Spring = March–May, summer = June–August, autumn = September–November, winter = December–February; numbers above bars indicate *n*; error bars represent standard deviation, consumptive mortality error bars are represented by dashed line, nonconsumptive mortality error bars represented by solid line, plus bars shown only.

Table 6. Generalized least squares (GLS) regression analysis of weekly LOESS-smoothed *C. helgolandicus* consumptive mortality rates of CV-♀ and CV-♂ stage-pairs with temperature and predators (January–December 2013): coefficients, standard error (SE), *t*-value, *p*-value and AIC value, single and multi-variable GLSs; SST = sea surface temperature; $n = 21$ (CV-♀), $n = 17$ (CV-♂); all abundances were $\log_{10}(x + 1)$ transformed except for CV-♀ with chaetognath abundance.

Stage and Sex	Model predictor(s)	Coefficient (slope)	SE	*t*-value	*p*-value	AIC
CV-♀						
	Chaetognath abundance	0.006	0.002	2.667	0.009	−425.6
CV-♂						
	SST	−0.027	0.011	2.450	0.027	−18.2
	Chaetognath abundance	0.092	0.037	2.502	0.020	−15.2
	Siphonophore abundance	0.086	0.014	6.152	0.00001	−27.8
	SST+	0.036	0.010	3.667	0.002	−13.1
	medusae abundance	−0.012	0.044	−2.634	0.020	

Both CV-male and CV-female VLT mortality rates were significantly positively related to temperature. There may be several factors behind this. First, the abundance, activity, and food demand of their predators is likely higher in warmer conditions. Second, higher metabolic rates of *C. helgolandicus* would be expected to result in higher intrinsic mortality and shorter life span of adults.

Considering the effects of predators, chaetognaths, siphonophores and total gelatinous zooplankton abundance were all significant predictors of late-stage *C. helgolandicus* VLT mortality rates. Analysis of the separate 2002–2004 and 2012–2013 datasets suggested that chaetognaths and siphonophores were most influential during the earlier time period, and medusae were more important during the latter. This suggests that there are interannual fluctuations in the predatory influence of each of the gelatinous zooplankton, and in some years, we see blooms of various medusae that may significantly impact the copepod population. We have performed simple calculations based on published feeding rates of the gelatinous predators (chaetognaths; Saito and Kiørboe (2001); siphonophores, Purcell (1982)) and find substantial daily removal during the summer months, sometimes exceeding > 100% of the standing stock of *C. helgolandicus* copepodites. These calculations have strong caveats based mainly around food selectivity, but support our correlative approach that gelatinous predators are the major elements in the variability in mortality observed at L4.

Parasagitta setosa and *Parasagitta elegans* are the two dominant chaetognaths recorded at L4. *Parasagitta* spp. are major predators of copepods (Rakusa-Suszczewski 1969), indeed *Calanus* spp. have been found to predominate in the diet of *P. elegans* in particular (Grigor et al. 2015). Various studies have linked *C. helgolandicus* abundance with chaetognath abundance (Southward 1984; Clark et al. 2003; Bonnet et al. 2010); and in addition Bonnet et al. (2010) using molecular gut content analysis found direct evidence of year-round ingestion of *C. helgolandicus* by *P. setosa*. Of the Siphonophora, the Calycophorae *Muggiaea atlantica* and *Muggiaea kochi* are the main species at L4. Blackett et al. (2014) found a positive correlation between *M. atlantica* and copepod abundance, suggesting that copepods are an important part of their diet. *C. helgolandicus* abundance was negatively related to siphonophore abundance in the 1989–2003 L4 study (Bonnet et al. 2010), indicating that siphonophores are capable of reducing copepod populations. There are ~ 35 species of Hydromedusae and Scyphomedusae recorded at L4, the majority of which have been reported to include copepods in their diet. The numerically dominant include *Aglantha digitale*, *Obelia* spp., *Liriope tetraphyllae*, and *Lizzia blondina*, with two of these, *A. digitale* and *Obelia* spp. recorded as feeding specifically on *Calanus* spp. (Lebour 1922). Ctenophores are dominated by *Pleurobrachia pileus* at L4 and are usually restricted to a month or so of extreme abundances in early summer. Although *P. pileus* are present for only a short period, their total number and biomass can be substantial, and numerous studies have highlighted their predation impact (e.g., Frank 1986; Gibbons et al. 2003).

There has been only limited mention in the literature of the relationship of *C. helgolandicus* abundance with fish larvae, despite this copepod species being recorded as a major prey item of many larval fish species (Lebour 1918; Rice 1963; Robb and Hislop 1980; Rowlands et al. 2008; Lynam et al. 2013). Our study found no relationships between fish larvae abundance (either total larval fish abundance [PML WP2] or MBA's YFT larval fish species data [MBA YFT]) and mortality rates. Although these predators may target *Calanus* spp., it may be that they are usually too rare to have a major impact on copepod abundances at L4.

Nonconsumptive vs. consumptive mortality rates

Our nonconsumptive mortality estimates are, to our knowledge, the first for a large copepod, and certainly for this species. Carcasses accounted for an average of 9% of the *Calanus helgolandicus* copepodites collected. This is similar to that found by Elliott and Tang (2011*a*), who reported a mean of 12–15% of *Acartia tonsa* copepodites being carcasses in the lower Chesapeake Bay, U.S.A. Nonconsumptive mortality of CI–CVI stages of *C. helgolandicus* contributed from 0% to 54% of total mortality, with a median of 4.4%, demonstrating that this type of mortality is not insignificant and at times can be substantial. Consumptive mortality of *C. helgolandicus* accounted for an average of 89% of the total mortality, which is somewhat higher, but comparable to the estimate of Hirst and Kiørboe (2002); that predation accounts for between approximately two-thirds and three-quarters of adult mortality in their study of global mortality rate patterns. Nonconsumptive mortality rates of total copepodites (CI–CVI) were high during the summer and winter, but decreased during late-summer to autumn, whereas consumptive rates tended to be much higher in the autumn. This indicates that in the autumn, at a time when predator abundance is at its highest, consumptive processes are the most important in controlling the *C. helgolandicus* population. At other times, nonconsumptive factors contribute more strongly (Fig. 6c). We stress here that our estimates are conservative because they make the simplifying assumption that copepods are retained in the water column through turbulent action after dying, rather than sinking to the benthos, which is unlikely for this large species.

Physico-chemical factors have been investigated as causative agents for nonconsumptive mortality. Elliott and Tang (2011*b*) established a positive relationship between *Acartia tonsa* nonconsumptive mortality and SST in Chesapeake Bay, and suggested that several mortality risk factors might increase with temperature, including disease and parasitism, starvation, and ageing. Other studies report no relationships between nonconsumptive mortality and environmental parameters (Tang et al. 2006; Beşiktepe et al. 2015). In our study, of those environmental factors considered, only maximum wind speed in the preceding 72-h was a predictor of total copepodite (CI–CVI) nonconsumptive mortality, suggesting that increased wind and storminess may play a role.

The occurrence of wind is a key factor in the generation of turbulence, as kinetic energy is added to the environment (Kiørboe and Saiz 1995). While small-scale turbulent eddies are known to enhance encounter rates and increase grazing rates (Alcaraz 1997), higher levels of turbulence can decrease the period of contact with food items (Prairie et al. 2012) and inhibit swimming, growth efficiency and development (Saiz and Alcaraz 1991; Saiz et al. 1992). Tank experiments simulating turbulence experienced in Lake Balaton (wind velocity of 11.8 ms^{-1}; $\sim$ 23 knots) found that the increased turbulence and low water-level ($\sim$ 4 m) caused a decrease in survival rates in the calanoid copepod *Eudiaptomus gracilis* (Tóth et al. 2011). Preliminary results from a recent study in Lyme Bay, UK following the procession of storms during the winter 2013/2014 found major decreases in abundance and diversity of seabed organisms at depths of 20–30 m due to the storm events (Sheehan et al. unpubl.).

The western English Channel frequently experiences gales and strong winds with a mean wind velocity > 40 knots and gusts exceeding 80 knots ($\sim$ 26 ms^{-1}), while the mean annual scalar wind speed at L4 has increased significantly from 1960 to 2014 ($R^2 = 0.75$, $n = 54$, $p < 0.00001$) (International Comprehensive Ocean-Atmosphere Data Set

(ICOADS); *COPEPOD: the global plankton database*. ONLINE. 2009. http://www.st.nfms.noaa.gov/copepod). The 50 m deep water column at L4 is well mixed in winter and too shallow to allow migration to deep water in winter, so it would be reasonable to hypothesize that copepod mortality due to extreme weather conditions may be important at certain times of the year. We suggest that the impacts of extreme episodic weather events on zooplankton, including their effects on mortality, merit further research (Tang et al. 2014).

Comparing mortality rates between sexes

A major aim of our study was to explore how the *Calanus helgolandicus* mortality rates (both consumptive and nonconsumptive) varied between the sexes. The proportion of adults which were dead at the point of their collection was generally greater for males than for females (Fig. 8). This result is akin to that reported by Elliott and Tang (2011*a*), with 40% of *A. tonsa* adult males collected and only 9% of adult females collected being carcasses. Based on VLT mortality methods, *C. helgolandicus* CV-male total mortality rates were $\sim$ 2.5 times greater than CV-female rates; a phenomenon that has been reported with other copepod species. For example, *Oithona similis* male mortality rates were estimated to be $\sim$ 12 times those of females in polar waters (Hirst and Ward 2008), and *Calanus pacificus* male mortality rates were 2–3 times higher than female rates in California (Ohman and Hsieh 2008).

The relative mortality rates of males and females reflect the assumption of a particular stage CV sex ratio. In this study, we have assumed a 1 : 1 sex ratio of CV copepodites. Many previous studies have also used this CV sex ratio (e.g., *C. finmarchicus* and *Pseudocalanus* spp., Ohman et al. [2002)]; *Oithona similis*, Hirst and Ward [2008]; *A. tonsa*, Elliot and Tang [2011*a*]). This assumption is in effect based on Fisher's principle (Fisher 1930), which states that most animal species must produce approximately equal numbers of males and females, and that any skew will adjust back to equal ratios through the process of natural selection. We highlight that there are various studies of CIV and CV sex ratios, but acknowledge that sexing of these stages is not simple, as *C. helgolandicus* CVs do not display obvious external secondary sexual characteristics (Green et al. 1993). However, analyses of gonad development and biometry have both been employed to sex late-stage copepodites. By calculating the ratios of sizes of body parts (i.e., metasome and urosome), two distinct size classes of *C. helgolandicus* CVs in the English Channel (Woodhead and Riley 1959) and *C. finmarchicus* CVs (Barnes and Barnes 1953) were observed. These size classes were attributed to the two sexes and indicated approximately equal sex ratios. Hirst et al. (2010) in their review of juvenile sex ratios, report near equal CV sex ratios for six calanoid copepod species, and following the sampling of copepods from L4, *Paracalanus parvus*, *Pseudocalanus elongatus*, and *Acartia clausi* CIV and CV stages were also found to have equal sex ratios. *Pseudocalanus minutus* CIV and CV sex ratios were also mostly equal (McLaren 1969). Our general conclusion is that for the *C. helgolandicus* CV stage, a 1 : 1 ratio may be generally valid. We note however, that Conover (1988) found that the sex ratio of *Calanus* CVs, based on the appearance of the gonad, was strongly skewed toward females, and more recent evidence reported a female-skewed sex ratio at birth in the calanoid copepod *Acartia tonsa* (Burris and Dam 2015), therefore, this assumption may need to be reviewed as new data come to light. Supporting Information Fig. S7 provides the male and female mortality rates derived using a female-skewed 5 : 1 CV sex ratio (based on the typical adult sex ratio found at L4). Such an assumption of course leads to an increase in CV-female mortality rates so that they are more comparable with CV-male rates.

The difference in copepod mortality rates between the sexes has been attributed either to male-skewed predation (MSP), defined as elevated consumptive mortality during more active mate-finding behavior; or the shorter life-expectancy exhibited by males and subsequent earlier death from natural causes (Hirst et al. 2010). The male-skewed predation theory purports that male copepods move more frequently and rapidly than females in their search for mates, and so are more likely to be detected by and to encounter predators (Kiørboe 2008; Kiørboe and Bagøien 2005). The shorter physiological longevity of males has been shown in various studies, and importantly *Calanus* spp. are believed to adopt a semelparous reproduction strategy (Mayor et al. 2009; Daase et al. 2014), defined as one single reproductive period in a lifetime (Hairston and Bohonak 1998), after which the adults die. This may contribute to some of the nonconsumptive mortality we see, particularly later in the season. Kiørboe et al. (2015) reported a consistent difference in senescence and average life spans of male and female planktonic copepods, with males aging faster and living shorter lives. Laboratory experiments with *C. helgolandicus* demonstrated that, in general, males moulted to adult and died in culture sooner than the females (Mullin and Brooks 1967). Male *Temora longicornis* were less sensitive (exhibited slower swimming velocities) to the presence of food than females (Moison et al. 2013) and gut fullness ratios were lowest in male *Calanus sinicus* (Chen et al. 2010), indicating that male copepods simply do not forage or ingest as much food as females. *Calanus finmarchicus* (Ohman et al. 2004) and *Calanus pacificus* (Ohman and Hsieh 2008) male mortality rates were explained by atrophied mouth-parts and reduced feeding rates of adult males, leading to an exhaustion of lipid reserves. Rodríguez-Graña et al. (2010) reported that males had more oxidative damage than females. Some studies question the male predation theory and suggest that differential longevity of the sexes is more important than previously considered (Gusmão et al. 2013). However, Hirst et al. (2010) found that predation accounted for $\geq$ 95% of

the mortality of the eight marine pelagic copepod species investigated and concluded that physiology alone could not explain sex-differentiated mortality in in the field.

By separating consumptive and nonconsumptive mortality rates for CV-female and CV-male *C. helgolandicus*, we found that consumptive mortality contributed most to the total mortality (at 70% and 85% of the annual mean rate for CV-females and CV-males respectively; Fig. 9). CV-male consumptive mortality rates were on average ~ 6 times greater than that of CV-females; whereas CV-male nonconsumptive rates were on average only twice that of CV-female rates. As death from senescence would result in carcasses, while predation typically does not, our results suggest consumptive mortality is of greater significance to male loss rates in comparison to that of females. Our approach provides a new method to explore differential causes of mortality in the sexes, and in this study provides evidence that predation on males is much greater than on females in *C. helgolandicus*.

Our investigation has improved our knowledge of *C. helgolandicus* mortality rates and the relative importance of consumptive vs. nonconsumptive death at the L4 site. The estimation of mortality rates and attributing causal factors is necessary to elucidate the important processes involved in regulating copepod populations. We conclude that total mortality rates are dominated by predation mortality, and gelatinous predators in particular are important in *C. helgolandicus* population regulation. However, nonconsumptive mortality is not inconsequential, and at times of the year this may contribute more than consumptive sources. Major agents of nonconsumptive mortality may include increased turbulence, which could become progressively more important in a future with a more extreme climate. *C. helgolandicus* males experience higher rates of both consumptive and nonconsumptive mortality than females. The sixfold difference between CV-male and CV-female consumptive rates indicates that predation may explain most of the elevated total mortality on males; however, the higher male rates likely reflect both their different behavior and their shorter physiological longevity.

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Conflict of Interest

None declared.

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